Revision of the South American freshwater fish genus *Sternarchorhamphus* Eigenmann, 1905 (Ostariophysi: Gymnotiformes: Apteronotidae), with notes on its relationships

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Abstract. — A revision of the apteronotid genus Sternarchorhamphus Eigenmann is presented. Sternarchorhamphus muelleri (Steindachner) from the Amazonas and Orinoco river systems, is redescribed and a lectotype is designated. Sternarchorhamphus hahni Meinken, a nominal species previously assigned to this genus, is transferred to another gymnotiform genus on the basis of evidence presented herein. As a consequence, Sternarchorhamphus is now considered monotypic. A brief discussion of Mago-Leccia's apteronotid subfamily Sternarchorhynchinae is provided and its monophyly is tentatively accepted. Relationships of Sternarchorhamphus muelleri within the Sternarchorhynchinae remain obscure, due to an absence of information on the phyletic history of closely related species, such as Orthosternarchus tamandua (Boulenger) and Ubidia magdalenensis Miles. A discussion on the taxonomic status of nominal species previously assigned to Sternarchorhamphus is provided.

Resumo. — Uma revisão do gênero de Gymnotiformes Sternarchorhamphus Eigenmann (família Apteronotidae) é apresentada. Sternarchorhamphus muelleri (Steindachner), das bacias dos rios Amazonas e Orinoco, é redescrita, e lectótipo é designado para esta espécie. Uma espécie nominal previamente referida a Sternarchorhamphus, S. hahni Meinken, é removida deste gênero; como conseqüência, Sternarchorhamphus é agora considerado gênero monotípico. Uma breve discussão sobre a subfamília de Apteronotidae proposta por Mago-Leccia, Sternarchorhynchinae, é apresentada, e sua monofilia é tentativamente aceita. A posição filogenética de Sternarchorhamphus dentro da subfamília permanece obscura, o que se deve, em parte, à ausência de informações sobre espécies relacionadas a S. muelleri, tais como Orthosternarchus tamandua (Boulenger) e Ubidia magdalenensis Miles. É feita uma discussão sobre o status taxonômico de espécies nominais previamente incluídas em Sternarchorhamphus.

The Neotropical gymnotiform genus Sternarchorhamphus Eigenmann (in Eigenmann & Ward 1905) was established to include three nominal species with elongate snouts, originally described in Sternarchus Bloch & Schneider (currently a junior synonym of *Apteronotus* Lacépède; e.g., Fowler 1951), namely: *Sternarchus* (*Rhamphosternarchus*) *macrostomus* Günther, 1870 (from Jeberos [=Xeberos], Río Marañon basin, Peru), Sternarchus (Rhamphosternarchus) muelleri Steindachner, 1881 (type species of Sternarchorhamphus; from the Rio Amazonas, at Pará State, Brazil), and Sternarchus tamandua Boulenger, 1898 (from the Rio Juruá, a tributary of the Rio Amazonas in Brazil). Eigenmann (in Eigenmann & Ward 1905:166), however, noted that this latter species was probably a member of "a genus distinct from Sternarchorhamphus as here understood" and, in fact, it was subsequently used by Ellis (1913) to establish the monotypic apteronotid genus Orthosternarchus.

The first appearance of the name Sternarchorhamphus was in a key to genera of Gymnotiformes ("Gymnotidae" of earlier authors) presented by Eigenmann & Ward (1905). An unequivocal citation present in that publication (p. 165) makes Eigenmann the sole author of the genus, according to Article 50a of the International Code of Zoological Nomenclature (1985). In that key, the new taxon was first included in the "Sternarchinae" (=Apteronotidae), and distinguished from Sternarchorhvnchus Castelnau on the basis of its "snout straight, the gape moderate," rather than "snout strongly decurved, mouth minute." Additionally, it was stated that Sternarchorhamphus seemed to be "intermediate between Sternarchus and Sternarchorhynchus, having the long snout of the latter and mouth size approaching the former" (Eigenmann & Ward 1905:165), a position also held by Ihering (1907).

Some years later, Meinken (1937) described *Sternarchorhamphus hahni* on the basis of a single specimen from the Rio Paraná drainage in Argentina. That was the first record of the genus outside of the Amazon basin. As discussed below, however, the examination of the holotype of *S. hahni* showed that it does not belong to the Apteronotidae.

Mago-Leccia (1976) first noted the presence of *Sternarchorhamphus* in the Río Orinoco system. He also proposed a phylogenetic scheme for Venezuelan gymnotiform genera where *Sternarchorhamphus* and *Sternarchorhynchus* were considered sistergroups within the Apteronotidae (Mago-Leccia 1976, fig. 99). Along with *Orthosternarchus* Ellis and *Ubidia* Miles, those two genera were assigned to the Sternarchorhynchinae (not of Hoedeman 1962), a proposed apteronotid subfamily whose members were recognized by their "very elongate snout and reduced mouth gape" (Mago-Leccia 1976:206; see also Mago-Leccia 1978:14 and Mago-Leccia 1994:13).

Campos-da-Paz (1992) had recently expressed some doubts about the monophyly of the *Sternarchorhamphus* plus *Sternarchorhynchus* clade, but tentatively recognized Mago-Leccia's subfamily Sternarchorhynchinae.

In a recent investigation, Triques (1993) did not find characters supporting a close relationship between *Sternarchorhamphus* and *Sternarchorhynchus*. Instead, he proposed *Sternarchorhamphus* as the sistergroup to a subunit of the Apteronotidae including the short-snouted genera *Adontosternarchus* Ellis, plus *Sternarchella* Eigenmann and *Porotergus* Ellis (Triques 1993: 123, fig. 24).

Mago-Leecia (1994) recently included two species in *Sternarchorhamphus: S. muelleri* and *S. hahni*. He stated in a footnote (p. 36), however, that this latter species could belong to a different gymnotiform genus, but without additional discussion. *Sternarchorhamphus macrostomus* was used by him to establish a new monotypic apteronotid genus, *Platyurosternarchus* Mago-Lecciã, whose relationships are currently unknown. The Sternarchorhynchinae appear only as part of a classificatory system proposed by Mago-Leccia (1978) (Mago-Leccia 1994:13).

The present study is a revision of *Sternarchorhamphus* Eigenmann. A detailed morphological description and osteological analysis of the type species, *S. muelleri*, is presented, along with data on geographic distribution based on recent collections from

the Amazon and Orinoco drainages. Reexamination of the holotype of *S. hahni* resulted in a transfer of this taxon to another gymnotiform genus.

Methods. — Most measurements were taken according to Mago-Leccia (1978) and were made point-to-point with dial calipers and ruler on the left side of specimens whenever possible. Measurements that require further explanation are the following: LEA (Mago-Leccia et al. 1985) is the distance from the tip of snout to posterior end of anal-fin base; interorbital width is the space between the dorsal margins of the eyes; head depth was taken at the occiput; and tail depth was measured at posterior end of the anal fin. "HL" denotes head length.

In the counts of pectoral-fin rays, the anterior unbranched rays are indicated by lower-case roman numerals, and branched rays are indicated by arabic numerals. The term "branched rays" refers to all rays posterior to the anterior unbranched rays, even if the posterior terminal ray is unbranched at its base or distal segment. All specimens with indications of regeneration and/or injuries at the posterior region of body were excluded from measurements of total length (TL) and tail length (CL), and counts of caudalfin rays. Morphometric and meristic data for the paralectotype of *Sternarchorhamphus muelleri* are given between brackets.

Osteological illustrations were prepared with the aid of a camera lucida, from a specimen cleared and counterstained for bone and cartilage with Alizarin red and Alcian blue respectively, according to the procedure of Taylor & Van Dyke (1985). Vertebral counts were made on this specimen and from radiographs of additional specimens, and follow Mago-Leccia et al. (1985). Bone terminology follows Mago-Leccia et al. (1985), except that the terms mesethmoid (e.g., Fink & Fink 1981) and anguloarticular (see Nelson 1973) were used instead of ethmoid and angular, respectively. In the list of material examined, "c&s" indicates a cleared and stained specimen.

Specimens examined for the present study are deposited in the following institutions: American Museum of Natural History, New York (AMNH). Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP), Instituto Nacional de Pesquisas da Amazônia, Manaus (INPA); Museu Nacional, Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP), Naturhistorisches Museum, Wien (NMW), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and Zoologisches Museum, Berlin (ZMB). In the "Material Examined" section, names of collectors are cited when known, and the term "EPA" refers to the "Expedição Permanente da Amazônia," a Brazilian field expedition under the direction of P. Vanzolini (MZUSP) fi-

nanced by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), São Paulo State Government.

Sternarchorhamphus Eigenmann, 1905

Sternarchorhamphus Eigenmann in Eigenmann & Ward 1905:160, 165-166, pl. VIII, fig. 7, partim, type by original designation Sternarchus (Rhamphosternarchus) muelleri Steindachner, 1881.-Ihering 1907, in key to "Gymnotidae," key to species of Brazil.-Eigenmann 1910, list of species.-Regan 1911, listed.-Ellis 1912, in key to "Sternarchinae."-Ellis 1913, in key to "Sternarchinae," described, food items, mutilation and regeneration of caudal peduncle. - Jordan 1920, listed, Eigenmann & Ward considered as authors.-Eigenmann & Allen 1942, in key to "Apteronotinae," briefly described, list of species.-Miles 1945, compared to Ubidia.-Miles 1947, compared to Ubidia.-Fowler 1951, Brazil, list of species.-Travassos 1960, synonymy, inclusion of S. hahni. - Géry & Vu-Tân-Tuê 1964, briefly compared to Gymnorhamphichthys Ellis, present in key to Apteronotidae, upper Amazon.-Britski

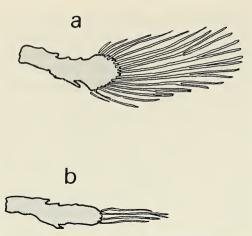


Fig. 1. Diagrammatic view of caudal-fin skeleton of apteronotid fishes. a. Widespread condition in the Apteronotidae (modified from Meunier & Kirschbaum, 1984:140, fig. 5a). b. Caudal-fin skeleton of *Sternarchorhamphus muelleri*.

1972, reported from Rio Paraná basin. – Mago-Leccia 1976, described from Venezuela, osteology, first record in the Río Orinoco basin, sister group of *Sternarchorhynchus*, assigned to the "Sternarchorhynchinae." – Mago-Leccia 1978, listed in the "Sternarchorhynchinae." – Bullock et al. 1979, listed. – Kramer 1990, discussion on electric organ discharge patterns. – Campos-da-Paz 1992, compared to *Sternarchorhynchus*. – Triques 1993, relationships, Rio Orinoco. – Mago-Leccia, 1994, diagnosis, brief description, notes on osteology, species.

Diagnosis. – According to recent studies on interrelationships of gymnotiform genera (Mago-Leccia 1976, Triques 1993; see also "Note on Relationships," below), the following characters are derived for *Sternarchorhamphus*, among closely related apteronotids: caudal-fin rays reduced in number (two to five rays; Fig. 1); presence up to five irregular rows of diminutive dentary teeth (most easily observed on the anterior portion of this bone in adults); presence of a mesocoracoid; and snout slightly turned dorsally.

The following combination of characters,

either primitive or of uncertain polarity, distinguishes *Sternarchorhamphus* from all other known apteronotids: snout elongated and laterally compressed; upper jaw produced and pointed, lower jaw somewhat included; teeth minute, present on both jaws at all ages; mouth small to moderate, 11.2– 16.5% [16.5%] in HL; eyes small, 2.5–4.4% [3.6%] in HL; lateral ethmoids present; scales rare or absent on antero-dorsal, and dorsal regions of body; dorsal fleshy filament originating on anterior third of total length and extending to vertical through posterior end of anal fin.

Etymology.—From *Sternarchus*, an earlier nominal genus of the Apteronotidae and currently junior synonym of *Apteronotus*, and the Greek *rhamphos*, for beak. Gender masculine.

Distribution. - Most examined specimens of Sternarchorhamphus were collected at localities near the main channels of the Rio Amazonas and Río Orinoco, and their large tributaries. Additional specimens came from the vicinities of Belém (Pará State, Brazil), Amapá (Amapá State, Brazil), and the Río Ucavali basin (Peru: Fig. 2). Mago-Leccia (1976) was the first to record Sternarchorhamphus from Venezuela, studying specimens from Río Portuguesa and Río Apurito. Recent collections from the Río Orinoco originated in the deep river channel (examined specimens from the Orinoco Delta and middle Orinoco, collected by the crew of R/V Eastward, 1978-1979, deposited at AMNH, ANSP, and USNM). Ellis (1913) and Santos et al. (1984) examined specimens from the Rio Tocantins basin.

Note on relationships. – Published phylogenetic hypotheses of the Apteronotidae do not include more than six of the ten currently accepted genera (e.g., Mago-Leccia 1976, Triques 1993) and, therefore, a comprehensive cladogram for the family is still unavailable (efforts on this subject are in progress elsewhere; J. Albert, and M. Triques, pers. comm.). It is beyond the scope

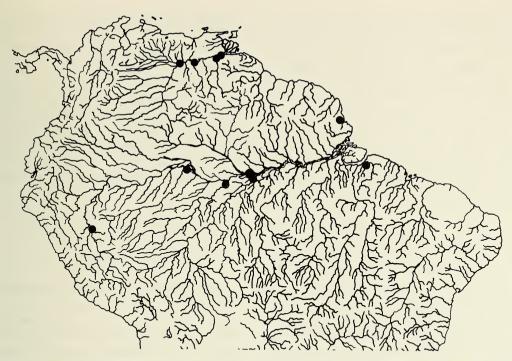


Fig. 2. Geographic distribution of *Sternarchorhamphus muelleri*. Some symbols represent more than one collection locality and/or lot of specimens.

of this study to present a detailed discussion on the intrafamilial relationships of the Apteronotidae. Furthermore, specimens of the apteronotids Orthosternarchus tamandua (Boulenger, 1898) and Ubidia magdalenensis Miles (1945) are extremely rare in collections, making it impossible to examine their internal anatomy and precluding a rigorous test of Sternarchorhynchinae monophyly (O. tamandua MZUSP 2647 [1 ex.] and U. magdalenensis USNM 123795 [1 ex.; paratype] were examined for external features).

The characters used by Mago-Leccia to define the Sternarchorhynchinae (1976), "reduced mouth gape" and "elongate snout," and to include *Sternarchorhampus* in it, are rather vague; their status as secondary homologues (=synapomorphies; see Pinna 1991) depends not much from their overall similarity, but rather on a well-corroborated hypothesis of relationships of closely related groups. An attempt to give these characters a more objective approach is presented below.

Sternarchorhynchines all have the mouth gape length less than 38% of the snout length. In remaining apteronotids, most gymnotiforms (except rhamphichthyids), and most closely related non-gymnotiform ostariophysans (Characiformes and Siluriformes; see Fink & Fink 1981), this value is consistently greater than 55%. When mouth gape length is compared to postorbital length, the value is always less than 31% in sternarchorhynchines, and greater than 40% in the proposed non-rhamphichthyid outgroups.

In most apteronotids, remaining gymnotiforms (but, again, not rhamphichthyids), and most closely related nongymnotiform ostariophysans, snout length represents less than 40% in head length. In Orthosternarchus, Sternarchorhamphus and Sternarchorhynchus this value is always greater than 50%; Ubidia, however, is a unique case. Although it also has a conspicuously elongate snout, the eye in this genus is located well forward in the head (an autapomorphic feature; see Mago-Leccia 1994:159, fig. 56B), resulting in the snout length/head length ratio decreasing to around 40%. Comparing snout length to postorbital length results in values of more than 90% for sternarchorhynchines (except *Ubidia* which, because of eye position, has the snout 70% of postorbital length) and less than 80% in remaining non-rhamphichthyid groups cited.

Currently available evidence indicates that the Rhamphichthyidae is distantly related to the Sternarchorhynchinae (Mago-Leccia 1976, 1978; Triques 1993), and the "reduced mouth gape" and an "elongate snout" can be hypothesized as being independently acquired in these taxa.

Some authors have called attention (e.g., Schaefer 1987) and discussed (e.g., Pimentel & Riggins 1987) the questionable general utility, in phylogenetic analyses, of proportional differences observed between morphological characters. It should be noted, however, that the above discussion is based on previous phylogenetic hypotheses concerning external (Fink & Fink 1981) and internal (Mago-Leccia 1976, 1978; Triques 1993) gymnotiform relationships. Furthermore, the utilization of morphometry in the present case is an attempt to make the terms "reduced" (the mouth) and "elongate" (the snout) as objective as possible (this kind of strategy is commonly observed in literature; e.g., Weitzman & Fink 1985 [fig. 79, characters 18, 32, and 40]). Additional justification for utilization of morphometry was found in Chappill (1989:231), who stated that "[q]uantitative characters should generally only be used [i.e., in phylogenetic analyses] when the choice is between examining them or abandoning the analysis entirely for want of sufficient characters." In some cases, however, there is evidence that morphometry can explicitly be used for phylogenetic purposes (e.g., Pinna 1989:24

[character 2], Costa 1990 [fig. 32, characters 13, 34, 39, 46, 80 and 89], Schaefer 1991 [fig. 15, character 13], and Vari 1991 [fig. 11, characters 17 and 42]).

In conclusion, the monophyly of the Sternarchorhynchinae, including *Sternarchorhamphus*, is tentatively accepted. The position of this genus within the subfamily, however, remains uncertain until additional material of related genera is available, which will allow a more detailed analysis of this question.

Sternarchorhamphus muelleri (Steindachner, 1881) Figs. 1-5, Table 1

- Sternarchus (Rhamphosternarchus) Mülleri Steindachner 1881:99, original description, Pará State, Brazil.—Steindachner 1882:15, pl. V, fig. 4, described, no exact locality, Rio Amazonas at Pará State, Brazil.
- Sternarchorhynchus mülleri (not S. mulleri Castelnau 1855).—Eigenmann & Eigenmann 1891:62, listed, Pará.—Eigenmann 1894:625, listed, Pará.
- Sternarchorhamphus mülleri. Eigenmann & Ward 1905:165-166, pl.VIII, fig. 7, assigned as type species of Sternarchorhamphus, original designation, Pará.-Eigenmann 1910:449, listed, Pará to Peru.-Ellis 1913:142-143, 174, 182-183, figs. 10 and 23-25, described, food habits, regeneration of caudal peduncle, Alcobaça (="Alcoboca"), Rio Tocantins, Pará.-Meinken 1937:79, compared to Sternarchorhamphus hahni.-Fowler 1939:276, Contamana, Peru.-Eigenmann & Allen 1942:320, listed, lower Amazon to the Ucayali.-Fowler 1945:180, fig. 65, Peru (Contamana) and Amazonas.-Miles 1947:184, compared to Ubidia magdalenensis.
- Sternarchorhamphus muelleri. Ihering 1907:277, Amazonas, Pará. – Mago-Leccia 1976:244–249, fig. 78, described from Río Orinoco, Venezuela. – Ortega & Vari

1986:12, Peru.—Campos-da-Paz 1992: 24, 134, briefly compared to *Sternar-chorhynchus*.—Mago-Leccia, 1994:35, 36, 71, 107, 156, 203, fig. 52, brief description, notes on osteology, listed.

- Sternarchorhamphus mulleri. Starks 1913: 23, described, variation of anus position, Pará. – Santos et al. 1984:18, 78, figure, in list of species from lower Rio Tocantins, common names, Brazil. – Triques 1993:91, listed, discussion of relationships to other gymnotiforms.
- Sternarchus mulleri. Jordan 1920:512, cited as type species of Sternarchorhamphus.
- Sternachorhamphus [misspelling] müelleri. – Magalhães 1931:178, cited.
- Sternarchus mülleri. Travassos 1960:24, cited as type species of Sternarchorhamphus.
- Sternarchoramphus [misspelling] mulleri. – Begossi & Braga 1992:107, tb.2, and 11, fig. 5, common name in Rio Tocantins, listed as fish avoided as food.

Material examined. - Brazil: NMW 65328:1, lectotype (photograph; new designation), 260.5 mm LEA, no exact collection site, Rio Amazonas at Pará State, F. Steindachner donation, accession file number "1874.I.299 & 299a"; NMW 65328:2, paralectotype, 249.0 mm LEA, same data of lectotype; INPA 4850, 7 specimens, Camaleão, Ilha da Marchantaria, Rio Solimões, Amazonas State, 3 Feb 1982, G. M. Soares; INPA 4852, 5 specimens, Camaleão, Ilha da Marchantaria, Rio Solimões, Amazonas State, 1 Jun 1981, G. M. Soares; MNRJ 1221, 1 specimen, no collection data; MNRJ 1222, 2 specimens, no collection data; MNRJ 9022, 2 specimens, 'Ver-o-Peso' market, Belém, Pará State, 10 Feb 1958, L. Travassos & F. Pires leg.; MNRJ 12182, 1 specimen, Amapá, Amapá State, Apr 1981, G. W. Nunan et al.; MZUSP 6983, 7 specimens, Rio Madeira, 25 km below Nova Olinda, Amazonas State, 27 Sep 1967, EPA; MZUSP 9580, 1 specimen,

fish market at Manaus, Amazonas State, 17– 19 Sep 1968, EPA leg.; MZUSP 23321, 1 specimen, mouth of Paraná do Catito, below mouth of Rio Juruá, Rio Solimões, Amazonas State, 4 Oct 1968, EPA; MZUSP 24675, 1 specimen, Santa Luzia, Rio Purus, Amazonas State, 11 Jan 1975, P. E. Vanzolini; USNM 52547, 2 specimens, Pará to Manaus, Rio Amazonas, 1901, J. B. Steere.

Peru: ANSP 95834, 2 specimens, Río Ucayali at Cantamana, Jul-Aug 1937, W. C. Morrow; ANSP 120348, 2 specimens, Pucallpa, on Río Ucayali, 18–19 Jun 1969, E. J. Huggins.

Venezuela: ANSP 149460, 3 specimens, shallow river, N side of river across from Isla Tres Caños, Delta Amacuro, 13 Nov 1979, R/V Eastward (H. Lopez, M. Corcoran); ANSP 149457, 1 specimen, Río Orinoco, below Barrancas, ca. km 140, depth 26 m, Delta Amacuro, 17 Feb 1978, R/V Eastward (Lundberg & Baskin); ANSP 160250, 6 specimens, Río Guariquito at confluence of Río Orinoco, Estado Bolivar, 25 Nov 1985, B. Chernoff et al.; ANSP 162297, 2 specimens, Río Orinoco, near mouth of Río Caura, Estado Bolivar, 22 Nov 1985, G. J. Lundberg et al.; ANSP 166792, 1 specimen, Caicara, L. Bartolico, Estado Bolivar, Río Orinoco basin, 20 May 1987, M. Rodriguez & R. Richardson; ANSP 166793, 1 specimen, Caicara, Castillero, Estado Bolivar, Río Orinoco basin, 19 Apr 1988, M. A. Rodriguez & A. Martinez; USNM 226339, 1 specimen, Río Orinoco, deep river channel, Brazo Imataca, 82 n.m. upstream from sea buoy, Territorio Federal Delta Amacuro, 22 Feb 1978, D. Taphorn; USNM 226491, 2 specimens, Río Orinoco, deep river channel, north side of Isla Tortola, 123 n.m. from sea buoy, Delta Amacuro Fed. Territory, 19 Feb 1978, J. N. Baskin; USNM 226495, 3 specimens, Río Orinoco, Brazo Imataca, south from Isla Remolino, ca. km 82.9 from sea buoy, Delta Amacuro Fed. Territory, 22 Feb 1978, Baskin/Lundberg; USNM 228805, 6 specimens (1 C&S), across from Palua, ca. 182

Table 1.-Morphometric data for the paralectotype (NMW 65328:2) and additional non-type material of *Sternarchorhamphus muelleri*. TL, LEA, HL, and CL are expressed in mm; measurement 1 is expressed as % of TL; measurements 2 to 7 are expressed as % of LEA; 8 to 21 as % of HL; 22 as % of CL. *SD*, standard deviation; and *n*, number of examined specimens.

	Paralectotype	Range	X SD	n
TL	292.0	261.0-446.0		15
LEA	249.0	188.0-375.0		17
HL	30.0	20.5-63.3		28
CL	43.0	35.0-77.0		15
1) Standard length	85.2	81.4-88.2	83.9 ± 1.7	15
2) Anal-fin length	90.4	89.1-93.0	91.2 ± 1.1	15
3) Body depth	10.1	8.7-12.2	10.2 ± 0.8	18
4) Head length	12.1	11.4-14.5	12.4 ± 0.9	18
5) Pre-anal distance	9.3	8.0-10.8	9.1 ± 0.7	18
6) Pre-pectoral distance	12.7	11.3-15.4	12.7 ± 1.1	18
7) Tail length	17.2	16.7-22.7	19.5 ± 1.9	14
8) Snout length	49.5	45.9-52.9	49.3 ± 2.0	28
9) Eye diameter	3.6	2.5-4.4	3.3 ± 0.4	28
10) Mouth width	16.5	11.2-16.5	13.3 ± 1.4	25
11) Interorbital width	11.9	8.0-13.0	10.6 ± 1.4	28
12) Snout to occiput	90.1	83.5-91.7	87.4 ± 2.3	28
13) Postorbital distance	53.4	46.9-53.8	50.5 ± 1.9	28
14) Pectoral-fin length	45.2	43.5-59.0	50.9 ± 5.2	28
15) Pre-anal-fin length	75.9	68.8-79.8	72.9 ± 2.6	26
16) Snout to anus	58.7	48.5-60.2	54.8 ± 3.5	27
17) Anterior naris-posterior naris	5.6	3.3-5.6	4.3 ± 0.6	26
18) Posterior naris-eye	25.7	22.0-30.3	26.8 ± 2.1	26
19) Head depth	62.0	52.1-63.9	57.6 ± 3.8	26
20) Head width	24.1	22.2-29.9	25.1 ± 1.9	28
21) Branchial opening	19.4	15.6-19.4	17.2 ± 1.2	28
22) Tail depth	9.7	6.3-10.6	8.2 ± 1.3	14

n. m. from sea buoy, 9 Nov 1975, H. Lopez & O. Riviero; USNM 228806, 6 specimens, shallow river, downstream from sea buoy 82, near mouth of a small caño, Delta Amacuro Fed. Territory, 21 Nov 1979, H. Lopez et al.; USNM 228808, 1 specimen, shallow river, north shore, 49 n. m. from sea buoy, Delta Amacuro Fed. Territory, 20 Nov 1979, Lopez et al.

Diagnosis. - As for the genus.

Description. – Morphometric data for the paralectotype (NMW 65328:2) and additional specimens of *S. muelleri* are given in Table 1. The lectotype (NMW 65328:1) is shown in Fig. 3.

Body strongly compressed laterally, especially posterior to abdominal cavity, deepest in this region; dorsal profile from nearly straight to gently convex. Lateral line complete, extending to caudal peduncle, but not onto caudal fin in some specimens.

Head laterally compressed, more markedly so anteriorly, deepest at occiput and widest in opercular area; snout pointed and conical, slightly turned dorsally in most specimens; eyes reduced in size, completely covered with skin, located dorso-laterally on head; small (paired) sensory pore present, dorsal to eye and usually near vertical through anterior border of eyes.

Mouth small, sub-terminal (inferior in some specimens), its gape usually not reaching vertical through anterior border of anterior nare; upper jaw projected, lower jaw somewhat included. Single patch of numerous diminutive conical teeth present on pre-

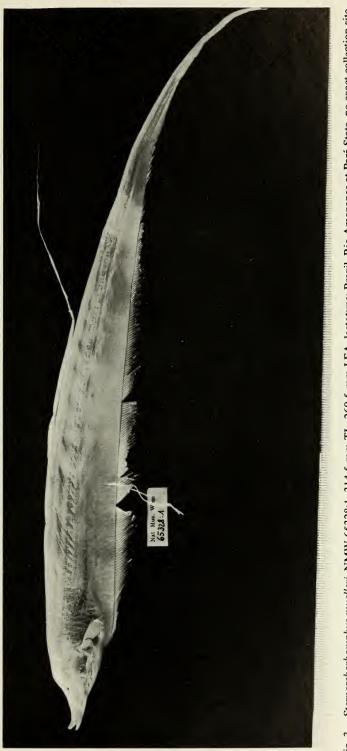


Fig. 3. Sternarchorhamphus muelleri, NMW 65328:1, 314.5 mm TL, 260.5 mm LEA, lectotype; Brazil, Rio Amazonas at Pará State, no exact collection site.

maxilla (25–40, $\bar{X} = 34.1$, n = 7 [approx. 35 in paralectotype]). Usually four of five irregular rows of similar teeth on dentary (25–45, $\bar{X} = 36.4$, n = 7 [approx. 25 in paralectotype]). Maxilla and mesopterygoid edentulous. Small rounded papillae covering part of the roof and floor of the oral cavity. Anterior nares tubular; posterior ones rounded, without a tube and remote from eyes.

Branchial opening reduced to a short slit immediately anterior to pectoral-fin origin; branchial membranes joined or partially joined to isthmus. Anterior chamber of gas bladder small, posterior elongate. Anus and urogenital papilla adjacent and located ventral to opercular region, shifting anteriorly with age.

Pectoral fins moderate, elongate and slightly pointed, with ii + 12–14 rays [ii + 13]. Anal fin with 230–262 rays [231], its origin near vertical through nape; first anterior anal-fin rays less developed (some undivided) and smaller than posterior ones.

Scales small, cycloid, absent or greatly reduced in number on anterior region of body and dorsally; lateral line perforated scales usually larger than those immediately dorsal and ventral to it. Scales above lateral line four to nine. Small scales, sometimes in single series, present on caudal fin in some specimens.

Dorsal filament (="dorsal thong"; a modified muscle according to Mago-Leccia 1994) originating on anterior third of total length, its tip reaching vertical through posterior end of anal fin. Tail (region from base of last anal-fin ray to tip of caudal fin) elongate, laterally compressed, ending in reduced caudal fin with two to five rays [four]; condition unique among Gymnotiformes. Caudal peduncle sometimes with discrete constriction at caudal-fin base.

Osteological features of *Sternarchorhamphus muelleri*, relevant at the generic level, are as follows: premaxilla broadest anteriorly, and extending posteriorly to near the maxilla; maxilla elongate and curved posteriorly, its anterior portion well-developed

(Figs. 4 and 5): dentary large, extending posteriorly and covering anterior portion of retroarticular: Meckel's cartilage well-developed and elongate, partially associated with anguloarticular and dentary: coronomeckelian bone reduced in size, compared to adjacent bones: retroarticular well-developed. with pointed antero-ventral process; lateral ethmoids present: vomer elongate, its anterior portion "arrow-shaped" and contacting parasphenoid through small cartilaginous bridge: posterior end of vomer pointed: palatine cartilage present, well-developed anteriorly and contacting anterior portion of maxilla: mesopterygoid broad. edentulous, with poorly-developed ascending process; parasphenoid elongate, bifurcate anteriorly and posteriorly: infraorbital series represented only by canal-bearing portions of bones; mesethmoid elongate, rounded and reduced at its anterior portion: two cranial fontanels present and well-developed (interfrontal larger than interparietal); supraoccipital small, with reduced crest; posttemporal fossae absent; opercle ornamented with numerous small trabeculae; mesocoracoid present; scapular foramen absent; coracoid with well-developed postero-ventral process, but not reaching cleithral symphysis; posttemporal fused to supracleithrum; extrascapular present; two postcleithra; four pectoral radials; four branchiostegal rays, first and second almost filamentous, others large and laminar; urohyal broad and expanded posteriorly with reduced head, and approaching in size the basihval and first ceratobranchial; gill rakers not ossified; four infrapharyngobranchials, fourth one cartilaginous; five epibranchials, fifth one cartilaginous; upper pharyngeal tooth plate with seven or eight teeth, connected to third epibranchial through a ligament; lower pharyngeal tooth plate with 12-13 teeth; Weberian apparatus without claustrum; 16-17 precaudal vertebrae (Weberian complex included); two "rib-like bones" (modified ribs?) present in posterior wall of abdominal cavity, anterior one enlarged, laterally compressed and turned an-

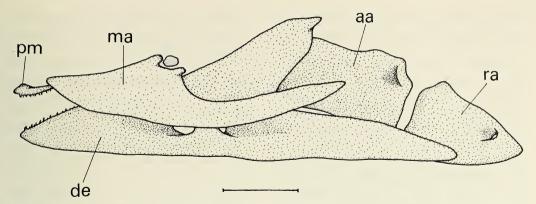


Fig. 4. Jaws of *S. muelleri*, USNM 228805, 188.8 mm LEA. Lateral view of left side. Scale bar = 1 mm. aa, anguloarticular; de, dentary; ma, maxilla; pm, premaxilla; ra, retroarticular.

teriorly; proximal pterygiophores of anal fin with expanded, pointed, symmetric projections anteriorly, directed dorsally on the anterior third of pterygiophore, well-developed posterior to abdominal region; 91–99 vertebrae to base of last anal-fin ray (Weberian complex included); well-developed intermuscular bones, especially conspicuous dorsally and ventrally to vertebral column, and posterior to abdominal region; caudal-fin skeleton consolidated into a single element of reduced size.

Color in alcohol.—Body light yellowish brown, covered with diminutive irregular dark spots (chromatophores), most on dorsal portion of head and snout, and on back. The overall coloration can vary from pallid to melanistic. Pectoral fins hyaline at base, and usually dark distally (chromatophores on fin membranes); anal fin of some specimens with continuous black margin along entire length, with melanophores also present over fin membranes; specimens from the Río Orinoco, however, can be nearly completely pallid (J. Lundberg, pers. comm.). Caudal fin hyaline.

Food habits. — Stomach-contents of Sternarchorhamphus showed fragments of partially digested insect larvae (tentatively identified as Diptera), along with some unidentified Annelida. These findings agree with those by Ellis (1913:174), who had also

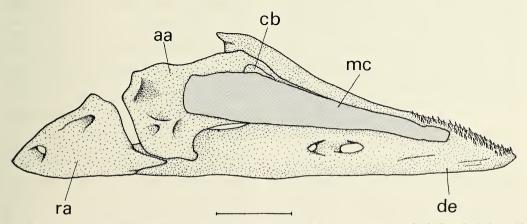


Fig. 5. Lower jaw of *S. muelleri*, USNM 228805, 188.8 mm LEA. Medial view of left side. Scale bar = 1 mm. aa, anguloarticular; cb, coronomeckelian bone; de, dentary; mc, Meckel's cartilage; ra, retroarticular.

noted a single unidentified Entomostraca specimen and additional insect larvae, other than Diptera.

Remarks. - Santos et al. (1984) listed the names "ituí" (a common name for most apteronotid fishes in Brazil) and "tuvira" (also used for other Gymnotiformes, except the Electrophoridae) for S. muelleri in the lower Rio Tocantins region. The same authors also observed that this species is the only apteronotid with some commercial value as a food fish in that area. Begossi & Braga (1992), curiously, listed S. muelleri as a fish avoided as food by local fishermen at Rio Tocantins (in States of Maranhão and Tocantins), and recorded the common name "lampréia" to this species (that name is also assigned for other non-apteronotid gymnotiform fishes occurring in that area).

Langner & Scheich (1978) and Kramer (1990) discussed the electric organ discharges (EODs) of some gymnotiforms, including specimens they identified as *Sternarchorhamphus*, which showed a fundamental frequency of EOD between 1300 and 1700 Hz. A figure presented by Langner & Scheich (1978:236, fig. 1), and later reproduced by Kramer (1990:198, fig. 4.57), however, does not show *Sternarchorhamphus*, but *Sternarchorhamphus*.

Etymology.—Steindachner proposed the name *Mülleri* (the original spelling in his 1881 paper) for the new species in honor of Johannes Müller, a famous German ichthyologist of the 19th century. Several different spelling forms for this species are currently widespread in literature (see synonymy, above). According to the International Code of Zoological Nomenclature (1985; Article 32d), however, the correct form is *muelleri*.

Taxonomic status of Sternarchus (Rhamphosternarchus) macrostomus Günther, Sternarchus tamandua Boulenger, and Sternarchorhamphus hahni Meinken

Günther (1870) described Sternarchus (Rhamphosternarchus) macrostomus ("ma-

crostoma" in the original spelling; not Sternarchus macrostomus Fowler [1943]) on the basis of a single specimen from Jeberos (=Xeberos), Río Marañon drainage, Peru, This nominal species was subsequently assigned to Sternarchorhvnchus by Eigenmann & Eigenmann (1891; "Upper Amazon"). Eigenmann (in Eigenmann & Ward 1905) included S. macrostomus in Sternarchorhamphus, without any detailed explanation. Ellis (1913) did not examine specimens of S. macrostomus and simply quoted Günther's original description, following Eigenmann's placement of the species. This view remained unalterated since then, until the recent work of Mago-Leccia (1994), who used the species to establish the monotypic apteronotid genus Platvurosternarchus.

Platyurosternarchus first appeared in a key to apteronotid genera (Mago-Leccia 1994: 26). Later, in the same study, that author stated that the genus was "proposed in order to locate properly the species Sternarchus macrostomus," that the new genus is "clearly different from Sternarchorhamphus" (p. 37), and provided a photograph of the head of a specimen from the Orinoco basin (p. 160, fig. 57A). A list of distinctive features (including uniquely derived characters, such as the overall morphology of caudal fin) was also given by Mago-Leccia, who definitely demonstrated that P. macrostomus and S. muelleri are different species (but note also characters already pointed out by Günther 1870). Relationships of Platyurosternarchus, however, were not discussed in that work, and the closest relatives of that genus remain uncertain. A preliminary view of this problem suggests that Platyurosternarchus and Sternarchorhamphus belong to different subsets within the family Apteronotidae and are not sister groups. As in S. muelleri, the snout in P. macrostomus is elongate (around 50% in head length), but the latter species does not have the reduced mouth gape length characteristic of sternarchorhynchines (approximately 65% in snout length, and 75% in postorbital length vs. less

than 35% in snout length, and less than 31% in postorbital length, respectively). The possibility of *Platyurosternarchus macrostomus* constitutes the sister-group of the Sternarchorhynchinae cannot be dismissed at this time, but further detailed investigation is needed (see discussion on the Sternarchorhynchinae, above).

Sternarchus tamandua was described by Boulenger (1898) on the basis of a single specimen, with an injured tail, from Rio Juruá (Brazil). The species was transferred to Sternarchorhamphus by Eigenmann (in Eigenmann & Ward 1905), who was followed by Ihering (1907) and Eigenmann (1910). Later, the species was used by Ellis (1913) to establish the monotypic apteronotid genus Orthosternarchus. The name of this genus, however, appeared first in key to genera to "Gymnotidae" (=Gymnotiformes) from British Guiana provided by Ellis (1912; type-species' name was not mentioned), and that should be considered its original description. Curiously, not a single specimen of Orthosternarchus was recorded from Guiana until the present date. Little has been published on this poorly known species since then, mainly because of its scarcity in collections. Detailed information on its internal morphology and osteology is unavailable. The overall form of the snout is an autapomorphic feature, clearly suggesting that O. tamandua is not conspecific with S. muelleri or any known apteronotid (see, for example, Ellis 1913: 144, fig. 11, Mago-Leccia 1994:147, fig. 41). Since this genus is currently assigned to the Sternarchorhynchinae, the possibility of Orthosternarchus and Sternarchorhamphus are its sister-groups must be left open until enough material is available to allow this kind of investigation. If a sister-group relationship between these two genera can be demonstrated, then an interesting taxonomic question will arise, since their included species were once referred to a single genus. Sternarchorhamphus. Current available evidence is scarce and cannot definitively show

a close relationship between *O. tamandua* and *S. muelleri*, so these species are here kept in their own separate genera.

A study on the single known specimen of Sternarchorhamphus hahni Meinken (holotype, ZMB 31367), collected near Corrientes, Rio Paraná basin in Argentina, revealed that it lacks the diagnostic features of the Apteronotidae (e.g., caudal fin internally supported by a single bony element; a dorsal fleshy filament) and should rather be referred to Rhamphichthys Müller & Troschel, 1846 (Rhamphichthyidae). In addition to several features observed only in rhamphichthyids and closely related groups among gymnotiforms (Hypopomidae: see Mago-Leccia 1978, and Triques 1993; e.g., no teeth on both jaws; anterior nares not tubular and located close to upper lip), S. hahni has 323 anal-fin rays (330 recorded by Meiken 1937; vs. a maximum of 290 anal-fin rays in related groups), a condition apparently uniquely derived for Rhamphichthys (or a subset of it) among closely related taxa. Mago-Leccia (1976, 1994) previously posed some doubts on the taxonomic status of S. hahni but, because of lack of access to type material, did not discuss the question in greater detail (a more detailed approach on this subject is currently being published elsewhere; Campos-da-Paz & Paepke 1994).

In conclusion, it seems reasonable not to include the nominal species S. hahni Meiken and S. macrostomus (Günther) in Sternarchorhamphus which, otherwise, would make it non-monophyletic. Sternarchus tamandu Boulenger remains in Orthosternarchus Ellis until a detailed phylogenetic study on the Sternarchorhynchinae reveals its position regarding that genus. The solution presented herein is to consider Sternarchorhamphus a monotypic subunit of the Apteronotidae, comprising only S. muelleri (Steindachner). As discussed above, however, its phylogenetic relationships to other sternarchorhynchine apteronotid genera remains uncertain, depending on more complete and conclusive investigations than those presented so far.

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